A new 'South American ungulate' (Mammalia: Litopterna) from the Eocene of the Antarctic Peninsula

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Abstract: *Notolophus arquinotiensis*, a new genus and species of the family Sparnotheriodontidae (Mammalia, Litopterna), is represented by several isolated teeth from the shallow-marine sediments of the La Meseta Formation (late Early–Late Eocene) of Seymour Island, Antarctic Peninsula, which have also yielded the youngest known sudamericids and marsupials. The new taxon belongs to the extinct order of 'South American native ungulate' Litopterna characterized by the convergence of the later forms with the equids and camelids. *Notolophus arquinotiensis* shows closest relationships with *Victorlemoinea* from the Itaboraian (middle Palaeocene) of Brazil and Riochican–Vacan (late Palaeocene–early Eocene) of Patagonia, Argentina. Although still poorly documented, this new taxon shows that the early Palaeogene Antarctic faunas might provide key data concerning the problems of the origin, diversity and basal phylogeny of some of the 'South American ungulates' (Litopterna). This new taxon shows the importance of Antarctica in the early evolution of the ungulates and illustrates our poor state of knowledge.

Initial palaeontological work in early 1980 on Seymour Island produced a modest assemblage of terrestrial fossil mammals (marsupials and South American ungulates). During the 1989–1990 season, geologists of the Instituto Antártico Argentino, while mapping Eocene marine rocks in Seymour Island, discovered small- and medium-sized land mammals, including two representatives of the South American native ungulates, Litopterna and Astrapotheria (Marenssi *et al*. 1994 and see also Hooker 1992). The Antarctic litoptern was referred by Bond *et al*. (1990) to the eolitoptern sparnotheriodontid genus *Victorlemoinea*. Renewed field efforts on Seymour Island (1992–2000) greatly enhanced the original collection and the sites are known to contain a high number of sparnotheriodontids, as well as many other taxa previously unknown from the area (Reguero *et al.* 2002). This new material allows us to reinterpret the teeth initially attributed to *Victorlemoinea*.

Litopterna is considered a natural group of South American native ungulates. Miocene–Pleistocene forms show a notable convergence with equids (Proterotheriidae) and camelids (Macraucheniidae). One of the most unusual of the litopterns was the Pleistocene camel-like *Macrauchenia* with large size and proboscis. The early Palaeogene forms (Palaeocene–Eocene) show morphological resemblances with the 'ancestral ungulates', the 'condylarths'. Sparnotheriodontids were medium- to large-sized ungulates. The family is known in the middle Palaeocene Itaboraian South American Land Mammal Age (SALMA) of Brazil and the late Palaeocene Riochican SALMA of Patagonia, and survived through at least the Late Eocene (Divisaderan SALMA) of Mendoza, Argentina. The species of sparnotheriodontids are classified in three genera and are listed in the Table 1.

The fossil record of the family Sparnotheriodontidae in South America is rather sparse;

Table 1. *Sparnotheriodontid species formally recognized*

Species	Geographic location	Age	Source
Victorlemoinea labyrinthica	Cañadón Vaca, Chubut	Riochican	Ameghino 1901
Victorlemoinea prototypica	Itaboraí, Brazil	Itaboraian	Paula Couto 1952
Sparnotheriodon epsilonoides	Cañadón Vaca, Chubut	Vacan	Soria 1980*a*
Phoradiadus divortiensis	Divisadero Largo, Mendoza	Divisaderan	Simpson *et al.* 1962
Sparnotheriodontidae?			
Heteroglyphis dewoletzky	Cerro del Humo, Chubut	Mustersan	Roth 1899

Species of Sparnotheriodontidae known in South America (Argentina and Brazil). Data from Soria (2001).

sparnotheriodontids are seldom common in any given locality, even during the late Palaeocene (Riochican SALMA), when the group reached its climax.

The taxonomy of Sparnotheriodontidae remains contentious and is currently based solely on teeth. This family has long been the subject of discussion over its systematic position, generic content and nomenclatural priorities. The main causes of these problems are the uniformity of its dental morphology (taxonomic differences are often minor and easily confused with intraspecific variation) and the poor quality of type specimens. Originally considered by Ameghino (1901) as a member of the meniscotheriid condylarths, Simpson (1945, 1948) regarded *Victorlemoinea* as a primitive Macraucheniidae (Litopterna). Later, this genus was included in the enigmatic family Sparnotheriodontidae (Soria 1980*b*, 2001; Cifelli 1983*a*, *b*, 1993). Morphological evidence suggests that sparnotheriodontids are most closely related to other primitive litopterns such as the eolitoptern Anisolambdidae (Hoffstetter & Soria 1986; Soria 2001; Anisolambdinae of Cifelli 1983*b*). However, other morphological studies, based on tarsals, argue that the Sparnotheriodontidae belongs to the Didolodontoidea, a group included in the paraphyletic Condylarthra (Cifelli 1983*a*, *b*, 1993). As the association of tarsal and dental elements that supports this last statement is not clear we follow here Soria (2001), treating the Sparnotheriodontidae as eolitopterns closely related to the Anisolambdidae.

The new sparnotheriodontid sample is important for a number of reasons: (1) it is valuable for systematic evaluation of previously collected specimens; (2) it can be used to test previous hypotheses about the age of the terrestrial mammal-bearing horizons of La Meseta Formation; and (3) it provides for a more complete assessment of the biogeographic associations of the La Meseta terrestrial fauna.

Material and methods

Comparisons were made with specimens in the Vertebrate Palaeontology collections of the Museo de La Plata (MLP), Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN), Museo Nacional of Rio de Janeiro (MNRJ) and the American Museum of Natural History (AMNH). All Seymour Island specimens are housed in the Vertebrate Palaeontology collection of the MLP. All listed specimens were collected from Instituto Antártico

Table 2. *Dimensions of sparnotheriodontid teeth from Seymour Island, Antarctica. See abbreviations in the text*

Specimen	L (mm)	W (mm)
MLP 90-I-20-1	20	*c.* 20
MLP 90-I-20-3	15.8	12.7
M LP 90-I-20-5	*c.* 10.2	*c.* 10
MLP 91-II-4-1	21.7	12.6
MLP 91-II-4-5	10.90	6.70
MLP 92-II-2-135	–	–
MLP 94-III-15-3	10.8	8
MLP 95-I-10-6	25.6	*c.* 25
MLP 96-I-5-9	12.45	10.40
MLP 96-I-5-10	17.20	13.80
MLP 01-I-1-1	31	16.8
MLP 04-III-3-1	17.50	13.50

Argentino and División Paleontología de Vertebrados, Museo de La Plata localities designated by 'IAA' and 'DPV', respectively. Dry sieving and surface crawling were the primary techniques for specimen collection.

All measurements are reported in mm (Table 2). Terminology and measurements for litoptern teeth follow Nessov *et al.* (1998) and Soria (2001).

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; DGM, Divisao de Geologia e Mineralogia do Departamento Nacional da Producao Mineral, Rio do Janeiro, Brazil; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MNRJ, Museu Nacional do Rio de Janeiro, Brazil.

Material

Comparisons to other sparnotheriodontid taxa were made using the following specimens: *Victorlemoinea prototypica*, MNRJ 1470-V (holotype), right M3, MNRJ 1471-V (paratype), left M3, MNRJ 1472V, left M3, MNRJ 1477V, right M1 or M2 (DP4?), MNRJ 1481V, right p3, MNRJ 1484, left M1, MNRJ 1487V, left p3, MNRJ 1402V, right m2, MNRJ 1488-V, left p3, DGM 268-M, left dp3-m1?, AMNH 49816, left M3; *Victorlemoinea* sp., AMNH 28465, left m1 or m2; AMNH 28466, left M1 or M2, AMNH 28467, right m3; AMNH 28468, left M1; AMNH 28508, right p2?; AMNH 28515, right upper

premolar; AMNH 27895, right M3; MLP 61-VIII-3-163, fragmentary right upper molar; *Victorlemoinea labyrinthica*, MACN A-10671 (type), left P4-M1?; *Victorlemoinea emarginata*, MACN A-10672 (type), right M1–M2; *?Victorlemoinea longidens*, MACN A-10670 (type), right m1–m2?; *Sparnotheriodon epsilonoides*, MACN 18225 (holotype), incomplete lower jaw with left and right i1–m3; *Victorlemoinea* sp., MLP 66-V-12-1, right M3, MLP 66-V-12-2, right DP4-M2; *Phoradiadus divortiensis*, MACN 18061 (type), right M2–M3; MLP 87-III-20-7, left p4?; MLP 87-III-20-16, fragmentary rostrum with left and right I3–P3; MLP 87-III-20-17, right P4-M3; MLP 87-III-20-39, left m3; MLP 87-III-20-71, right P1–P3; MLP 87-III-20-72, very damaged skull and lower jaw with right P2–M3 and m2–m3 preserved; *Heteroglyphis dewoletzky*, MLP 12-1462 (type) left upper molariform.

Systematic palaeontology

Class MAMMALIA Linnaeus, 1758
Grandorder UNGULATA Linnaeus, 1766
Order LITOPTERNA Ameghino, 1889
Suborder EOLITOPTERNA Soria, 2001
Family SPARNOTHERIODONTIDAE Soria, 1980*a*

Emended diagnosis (after Soria 1980*a*)

Medium-sized (e.g. *Phoradiadus*) to large-sized (e.g. *Sparnotheriodon*) litopterns. Complete and closed dental series, i3/3, c1/1, p4/4, m3/3; teeth brachyodont, lophobunoselenodont to lophoselenodonts; i1–i3 relatively robust, foliform or spatuliform, increasing in size posteriorly (i1<i2<i3). The i3 is non-caniniform (e.g. *Sparnotheriodon*, *Phoradiadus*), lingual and labial cingula variably developed. The c1 are enlarged and conical (similar to those of the notoungulate Isotemnidae), with anterior and posterior crests, normally obliterated by wear, especially the anterior one; with labial and lingual cingula. Lower cheek-teeth (p1–m3) with labial and lingual cingula variably developed, but normally the lingual cingulum is weaker than the labial. The p1 is not molariform, simple and single rooted, elongated anteroposteriorly with a single main cuspid, prolonged by an anterior and a posterior crest or very short talonid. The p2 is more complex, with trigonid crescentic and short talonid (*Phoradiadus*) or trigonid and talonid subequal and bicrescentic (*Sparnotheriodon*).

The p3–p4 are molarized and, with the m1–m3, all are morphologically very similar, lophoselenodont and bicrescentic, dp4 fully molarized, with talonid and trigonid subequal (*Sparnotheriodon*) or trigonid somewhat smaller than the talonid (*Notolophus*), with well-developed labial (ectoflexid) and lingual (meta and entoflexid) flexids. Trigonid with a very well developed paralophid, its lingual end with a cuspid (paraconid? or ?neoparaconid) rapidly coalescent with wear. Metaconid high, but especially conspicuous on m1–m3 (e.g. *Sparnotheriodon*); lingual wall of the metaconid flattened, with descending crest enclosing part of the talonid basin that is more conspicuous on p3–p4. Talonid with cristid obliqua connected to the lingual end of the metalophid (metaconid). Entoconid very small (*Sparnotheriodon*) to well developed (*Phoradiadus*) and coalescent at the base with the hypoconulid (e.g. *Sparnotheriodon*). The m3 is larger than the m1 and m2, with talonid of m3 subequal to the trigonid or longer and narrower than the trigonid with a posteriorly projecting hypoconulid (e.g. *Notolophus*).

I1–I3 with lingual cingulum well developed. I3 equal or larger than the I1–I2. C1 very well developed, robust, similar to those of the Isotemnidae notoungulates, with sharp anterior and posterior crests (*Phoradiadus*). P1–P4 with labial and lingual cingula, variably developed, continuous or not. P1 simple, enlarged antero-posteriorly, with a single labial cusp, single rooted but bilobed lingually. P2–P4 increasingly complex and expanded transversally. P2–P3 with a labial (paracone) cusp showing no or very little differentiation of the metacone and a well-developed anterior parastyle. P2 with a very small protocone with anterior and posterior crests enclosing a basined trigon. The P3 is more complex, with a well-developed protocone, high and enclosing with the paraloph and metaloph a central fossette in the trigon basin. Paraloph connected to the ectoloph, with one or two cuspules trending lingually to the trigon basin from the ectoloph. Protostyle variably developed in the anterolingual cingulum. The P4 is molariform, with a metacone well differentiated, protocone very well developed and a crescentic metaconule. Lingual cingulum continuous or interrupted, always with well-developed pre- and post-cingulum, sometimes with a double cingulum. The M1–M2 with a strongly lophoselenodont ectoloph. Parastyle and mesostyle very well developed, with strong labial columns projected labially or anterolabially. Metastyle fairly to little developed. Paracone and metacone selenodont, with labial columns little developed or absent; projecting lingually into the trigon and variably developed

there are cuspules, forming one or two short crests. Protocone bunoid, connected by a short crest to the paraconule and to the hypocone, closing the internal valley, but with a shallow lingual sulcus. Hypocone smaller than the protocone and connected by a short crest to the metaconule (e.g. *Victorlemoinea*, *Phoradiadus*) or directly to it (*Notolophus*). Paraconule and metaconule subcrescentic, sometimes connected to the ectoloph by very short and low crests. In some cases (*Notolophus*) the paraconule is no longer recognizable as an independent cusp, present as a short paraloph connected to the anterior cingulum. Post-metaconule crista present but variably developed. Labial cingulum not very strong, sometimes restricted to the posterior portion; lingual cingulum variably developed. Precingulum, with a very well developed protostyle, sometimes connected to the paraloph (*Notolophus*). Post-cingulum encloses a low fossette. Pre- and post-cingulum present as a low extra cingulum, forming a 'double cingulum' that occurs also in the Anisolambdidae litopterns. The M3 is similar to the M1–M2, but with the hypocone absent. Of the deciduous molars known, the DP4 is fully molarized, with prominent mesostyle, hypocone, paraloph, metaloph, postcingulum fossette, accessory cusps projecting lingually from the ectoloph as a 'double post-cingulum'. As so far known, the recognized taxa in this family posses enamel with vertically oriented Hunter–Schreger bands.

Comments

Soria (1980*a*) established the Sparnotheriodontidae as an undetermined notoungulate monotypic family based on *Sparnotheriodon epsilonoides* from the Vacan subage (late Palaeocene–early Eocene) of Patagonia. Subsequently, Soria (2001) characterized the family and included with it the Anisolambdidae (regarded by Cifelli as a subfamily of Proterotheriidae) in a new suborder, Eolitopterna.

Cifelli (1993) defined the Sparnotheriodontidae by several advanced characters, including a lophoid metaconule and an expanded postcingulum, but included in this family the Indaleciinae, a group of very small ungulates traditionally considered as Adianthidae litopterns (Cifelli & Soria 1983) or as a family, Indaleciidae, of the Order Notopterna (Soria 1989). Bonaparte & Morales (1997) followed Cifelli (1993) in the grouping of *Victorlemoinea* and *Indalecia*, but considered them all litopterns. Here, we exclude the indaleciids from the Sparnotheriodontidae and, as stated earlier, we follow Soria (2001) in his use of the Sparnotheriodontidae.

Notolophus gen. nov.

Type species

Notolophus arquinotiensis, sp. nov.

Diagnosis

Same as for the type species.

Etymology

Notos, is derived from the greek νοτοσ, south, in reference to the geographical area where the taxon was found; and λοφοσ, lophs, crests.

Notolophus arquinotiensis sp. nov. (Figs 2a, b, 4a, c & 5a, b)

Holotype

MLP 95-I-10-6, left M3 incomplete (the buccal part of paracone and metacone is missing) (Fig. 2a). La Meseta Formation, Submeseta Member (TELM 7), DPV 16/84 locality. This molar was briefly described and figured by Vizcaíno *et al.* (1997).

Hypodigm

Holotype plus MLP 90-I-20-1, left upper molariform (M1 or M2?), *Cucullaea* I Member (TELM 5), IAA 1/90. MLP 91-II-4-1, right p4, *Cucullaea* I Member (TELM 4), DPV 2/84 locality. MLP 95-I-10-7, fragmentary left upper molariform, *Cucullaea* I Member (TELM 5), MLP 01-I-1-1, right m3, *Cucullaea* I Member (TELM 5), IAA 1/90 locality. MLP 04-III-3-1, incomplete right p4, *Cucullaea* I Member (TELM 5), IAA 1/95.

Referred specimens

MLP 90-I-20-3, right I3?, *Cucullaea* I Member (TELM 5), IAA 1/90 locality. MLP 90-I-20-5, left upper premolar incomplete (P2 or P3?), *Cucullaea* I Member (TELM 5), IAA 1/90 locality. MLP 91-II-4-5, right upper premolar (P1), *Cucullaea* I Member (TELM 5), IAA 1/90 locality. MLP 92-II-2–135, fragment of a molariform (lower?), Campamento Member (TELM 3), IAA 1/92. MLP 94-III-15-3, left lower incisive, *Cucullaea* I Member (TELM 5), IAA 1/90 locality. MLP 96-I-5-5, left upper incisiviform (I1?), *Cucullaea* I Member (TELM 5),

IAA 2/95 locality. MLP 96-I-5-9, left lower incisiviform or first premolar?, *Cucullaea* I Member (TELM 5), IAA 3/96 locality.

Type locality

Museo de La Plata locality DPV 16/84, Seymour Island, Antarctic Peninsula (Fig. 1). GPS data: 64°14′04.672″S and 56°39′56.378″W. Sr isotope dating from this horizon yields an age of approximately 34.2 Ma (Dingle & Lavelle 1998).

Additional specimens are known from other localities (Fig. 1) in lower levels (*Cucullaea* I and Campamento Members) of the La Meseta Formation.

Stratigraphy and age

La Meseta Formation (late Early Eocene–Late Eocene), Campamento (Early Eocene), *Cucullaea* I (Middle Eocene) and Submeseta (Late Eocene) members.
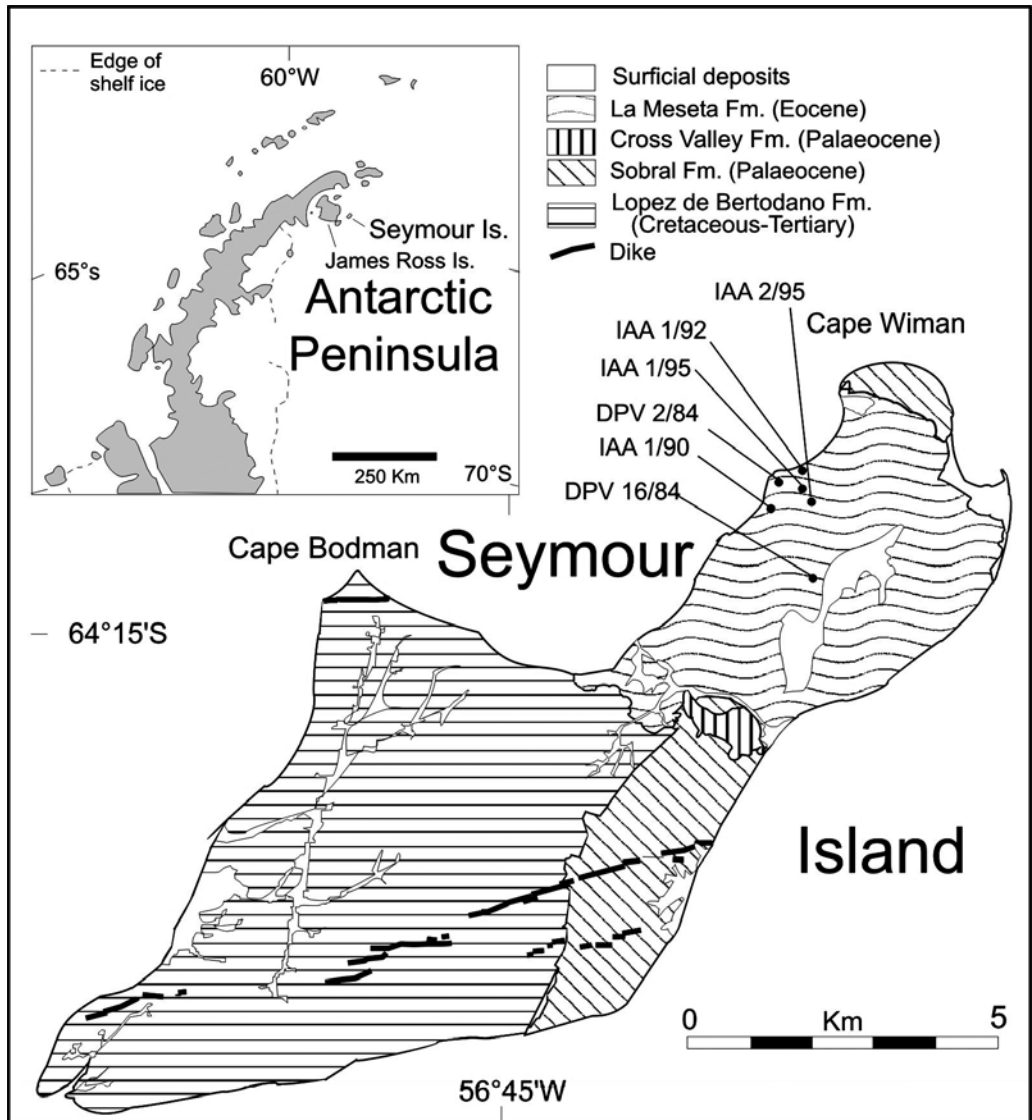
Fig. 1. Map of Seymour (Marambio) Island (Antarctic Peninsula) showing the IAA and DPV localities mentioned in the text.
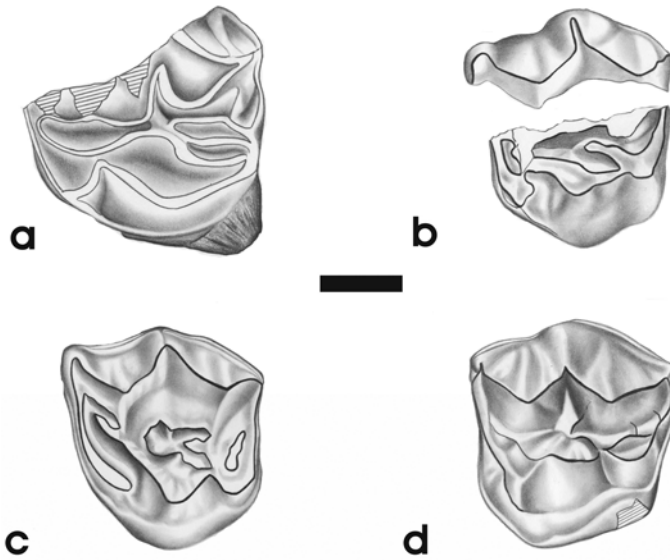
Fig. 2. Occlusal views of upper molars of sparnotheriodontids from Antarctica and Patagonia. (**a**) *Notolophus arquinotiensis*, gen. et sp. nov. MLP 95-I-10-6, left M3, holotype; (**b**) *Notolophus arquinotiensis*, gen. et sp. nov. MLP 90-I-20-1, left M1 or M2; (**c**) *Victorlemoinea labyrinthica*, MACN A-10871, left M1 (based also on M2 of the same individual); and (**d**) *Victorlemoinea* sp. MLP 66-V-12-2, right M1 (reversed). The scale bar equals 5 mm (drawing by A. Viñas).

Etymology

The specific epithet, *arquinotiensis*, is in reference to the Ihering's (1927) Archinotis continent.

Short diagnosis

A sparnotheriodontid larger than *Phoradiadus* and nearly equal as *Sparnotheriodon*. Differs from the other known taxa in having the upper molars with a protocone projected anteriorly by a short paraloph which connected to the protostyle in the second anterior cingulum (precingulum). Metaconule lophoid anteriorly extended and connected directly to the poorly developed hypocone, without intermediate crest as in the other taxa known. In the M3 the hypocone is very weak or absent, also the paraloph and the protostyle connects directly to the protocone. Lower molariforms with the trigonid smaller than the talonid. The m3 has a well-developed bunoid entoconid and a posteriorly projecting hypoconulid.

Differential diagnosis

Sparnotheriodontid much larger than *Phoradiadus divortiensis*, and nearly as large as

Sparnotheriodon epsilonoides. Upper molars with a very strong and well-developed ectoloph, labial cingulum very weak and restricted to the posterior portion of the ectoloph, between the metacone and the short metastyle. Short but strong lingual projections, one from the posterior part of the paracone and other from the anterior part of the metacone. Protocone elongated and projected anteriorly by a paraloph in which no paraconule is visible as separate cusp. Hypocone little developed connected by a short crest to the protocone; the hypocone is vestigial or absent on M3. Metaconule lophoid, nearly straight and very anteriorly extended, directly connected to the hypocone, without the short intermediate crest connecting these cusps as in *Victorlemoinea* or *Phoradiadus*. Post-metaconule crista low and post-cingulum enclosing a small basin that is not so developed as in *Victorlemoinea* or *Phoradiadus*. In the M3, the metaconule is connected with the first post-cingulum. The second anterior cingulum (or precingulum) possess a prominent protostyle, which is connected by a short posterolabial isthmus to the paraloph. In the M3 the protostyle directly connects to the anterior portion of the protocone, the paraloph being vestigial or absent.

Lower molariforms with trigonid somewhat smaller than the talonid. Trigonid and talonid

basins not so narrow and *Phoradiadus* and *Sparnotheriodon*. The trigonid exhibits a very well developed paralophid, with an engrossed lingual end that could represents a paraconid or ?neoparaconid. Posterior premolars with a conspicuous descending crest posterior to the metaconid; small entoconid connected with the hypoconulid. The m3 with a talonid larger and more elongated than the trigonid, with a projecting hypoconulid in a rudimentary 'third lobe'; well-developed bunoid entoconid antero-posteriorly enlarged and connected to the hypoconulid. Labial cingulum variably developed; lingual cingulum low and continuous to absent.

Description

As stated earlier, our knowledge of previously known Sparnotheriodontidae is meager. Taking this in account, the unassociated and, some-times, fragmentary nature of the Antarctic sparnotheriodontid specimens precludes an adequate interpretation. Most of the Antarctic ungulate teeth undoubtedly can be assigned to Sparnotheriodontidae, and with a high degree of confidence to *Notolophus arquinotiensis*. Notwithstanding, some of them are difficult to interpret, not in taxonomical reference but in its proper position in the dental series given the aforementioned scanty knowledge of the complete dental anatomy of this group.

The molariform teeth, upper and lower, can be referred with a high degree of confidence to this new taxon because all upper molars known have the same derived features. The lower molariform teeth match well in size with the upper ones and are therefore referred to the same taxon.

MLP 90-I-20-3 (Fig. 5) and MLP 96-I-5-10 are incisiviforms rather than caniniforms and match in size with the other teeth assigned to *Notolophus arquinotiensis*. They are robust, with a straight root and a labial single cusp with a convex labial wall (in MLP 90-I-20-3 the wear has obliterated this cusp). There are very well developed labial and lingual cingula. The enamel is thick with strongly marked alternat-ing bands of the vertically oriented Hunter–Schreger bands. The morphology of these teeth is very different from the incisors known of Pyrotheria and Astrapotheria (see Simpson 1967) (astrapotheres do not have upper incisors), which also have vertically oriented Hunter–Schregger enamel bands (see Fortelius 1985) as in the Sparnotheriodontidae. Also, these teeth resemble the I3 of some notoungulate families such as the Isotemnidae,

but the enamel structure of the isotemnids is completely different lacking the vertically oriented Hunter–Schreger bands (see Fortelius 1985). By comparison with the upper and lower incisors known in *Phoradiadus* and *Sparnotheriodon* we refer tentatively these specimens as probable upper incisors (I3?) of *Notolophus arquinotiensis*, but recognize that they are more robust than the I3 of these species. It cannot be ruled out that the teeth aforementioned could represent upper canines, but since in sparno-theriodontids, like *Phoradiadus divortiensis*, the canines (upper and lower) are pointed and with sharp edges, we therefore, identify these teeth tentatively as I3. MLP 96-I-5-5 is a very worn compressed mesiodistal incisiviform with an ellipsoid coronal figure, with no trace of a labial cingulum; it is very probably an anterior incisor, perhaps the I1. By comparison with the anterior lower dentition known in *Sparnotheriodon epsilonoides*, MLP 94-III-15-3 is considered as a probable lower incisiviform (right i3?); it is a simple tooth, very worn, with a principal labial cusp and a short anterior crest; there is also a lingual cingulum connected with the anterior crest and it has a middle lingual cuspule. The specimen MLP 96-I-5-9 very probably repre-sents a first lower premolar (left p?1); this tooth, although very worn occlusally, shows an antero-posteriorly enlarged and wide trigonid, with a principal labial cusp area and a very short talonid, somewhat different then to the more elongated p1 of *Sparnotheriodon epsilonoides*. This tooth is single rooted with a very oblique root. No teeth were found that could be referred confidently as the canines, upper or lower, of *Notolophus arquinotiensis*.

MLP 91-II-4-5 is a very simple tooth, single rooted, with a flattened crown by wear. It has a principal labial cusp (paracone) with a short anterolabial crest interpreted as a parastyle, and a shorter posterior crest (metastyle?). Labially, the principal cusp has a convex surface and an anterior shallow fold which delimitates the parastyle from the paracone. A strong lingual cingulum is connected to the parastyle and metastyle; this lingual cingulum has a well defined cuspule which is connected to the paracone by a short posterolabially directed crest. This tooth is interpreted here as a P1.

MLP 90-I-20-5, by comparison with the upper premolars of *Phoradiadus*, represents an upper premolar, possibly a left P3. The specimen is not complete, but has a well-developed protostyle, a bunoid protocone, apparently lacks the hypocone and short lingual crests project from the ectoloph, and the posterior fossette formed by the metaloph and posterior cingulum has

been obliterated by wear. Posterior to the cingulum there is an extra cingulum.

Sparnotheriodontid molars are quite uniform in form, and those of *N. arquinotiensis* share the same general pattern with other Patagonian sparnotheriodontids, but their proportions and especially the morphology of the upper molars is quite characteristic.

The holotype, MLP 95-I-10-6 (Fig. 2a), is of roughly rectangular outline, and the anterior and medium part of the ectoloph is missing. The preserved ectoloph shows a lophoselenoid metacone with a flattened labial area and a short metastyle which descends posteriorly; there is also preserved part of a low labial cingulum, but which may or may not have been continuous. The shallow internal basin or principal valley is formed between the protocone and the ectoloph, and exhibits two short, low crests projecting from the ectoloph. The protocone is large, anteroposteriorly elongated and connected to a very well developed anterolingual cusp. This lingually displaced cusp is interpreted here as an enlarged protostyle cingular cusp, although we do not rule out the possibility that it could also be a displaced paraconule fused with the protostylar cusp. Nevertheless, its position and the relationships with the second precingulum are more indicative of an enlarged protostyle. The protocone possess a posterior crest that connects to the post-cingulum. The metaconule is strongly lophoid and projected mesiodistally to the internal valley, post-metaconular crista well developed and directed labially connecting the metaconule to the metacone area. No hypocone exists, and the metaconule connects directly with the posterior projection of the protocone. The post-cingulum, connected to the protocone and metaconule, is expanded and encloses a small fossette; this basined post-cingulum is proportionally more developed in *Victorlemoinea* (Fig. 3) and *Phoradiadus* than in *Notolophus* (Fig. 2). Pre- and post-cingula with a very low extra cingulum. The lingual cingulum is very low and restricted to the anterior part of the protocone.

MLP 90-I-20-1 is very probably a left M1 or M2 (Fig. 2b), although it could represent a molariform DP4. It is very similar to the above described M3, but has a complete ectoloph. No labial columns are present on the paracone and metacone, and, except in the middle, which is slightly convex, the walls of the paracone and metacone are flattened to slightly concave. The parastyle is conspicuous, but the mesostyle represents the strongest element of the ectoloph with a very wide base. The labial cingulum is restricted to the posterior part of the
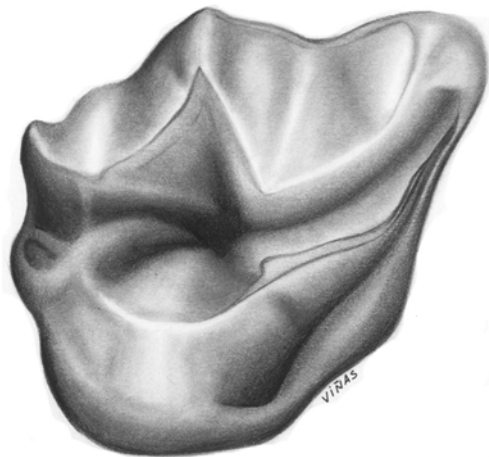

Fig. 3. Occlusal view of right M3 (MLP 66-V-12-1) of *Victorlemoinea* sp. The scale bar equals 5 mm (drawing by A. Viñas).

ectoloph. The hypocone is small and connected to the protocone by a short crest, with a very shallow sulcus between the protocone and hypocone. The metaconule is lophoid, strongly projected mesiodistally as in the M3, and is connected directly to the hypocone without the short intermediate lingually projected crest that connects the metaconule and hypocone in *Victorlemoinea* (e.g. *V. labyrinthica*) and *Phoradiadus*, but which is very short and nearly absent in MLP 66-V-12-2 (Fig. 2d) identified as *Victorlemoinea* sp. from the Vacan (early Casamayoran) of Patagonia. Post-metaconular crista is similar in form and direction as in the M3, although it is lower and not so well developed. Lingual cingulum apparently restricted to the anteriormost part of the protocone. Anterior and posterior cingula with low extracingula, conforming the double cingulum of the Sparnotheriodontidae.

Two lower molariforms, MLP 91-II-4-1 (Fig. 4c) and MLP 04-III-3-1, are tentatively assigned to the 'molarized' premolars of this species, and they probably represent two right p4, or a p4 and a p3, respectively. They are fully molariform with the trigonid crescent relatively shorter than that of the talonid and not so labially projected. The paralophid is very well developed and lingually projected as a small
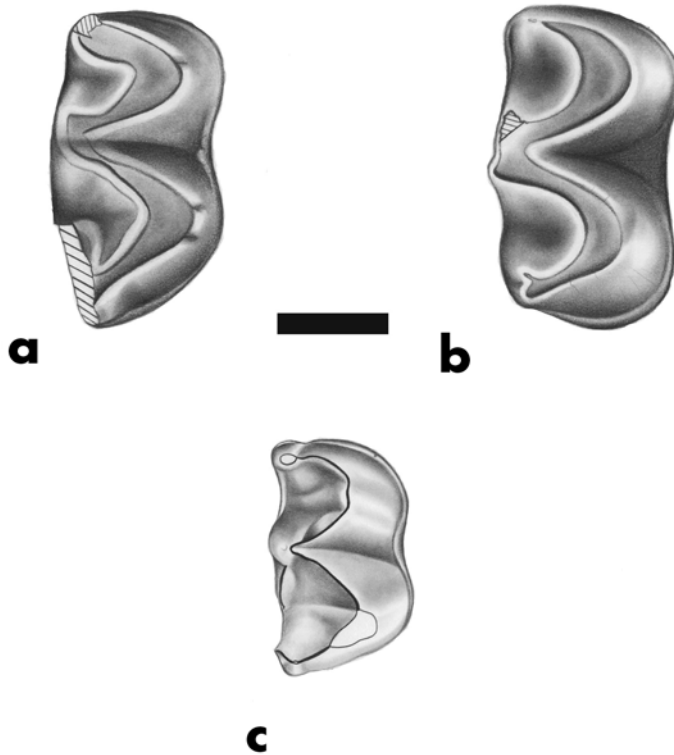
Fig. 4. Occlusal views of lower molars of sparnotheriodontids from Antarctica and Patagonia. (**a**) *Notolophus arquinotiensis*, gen. et sp. nov. MLP 01-I-1-1, right m3; (**b**) *Sparnotheriodon epsilonoides*, MACN 18225, right m3. The scale bar equals 5 mm (drawing by A. Viñas). (**c**) *Notolophus arquinotiensis*, gen. et sp. nov. MLP 91-II-4-1, occlusal view of right p4. The scale bar equals 5 mm (drawing by A. Viñas).

cuspid (paraconid or ?neoparaconid). Meta-conid with a very sharp descending crest, similar to that observed in the p3–p4 of *Sparnotheriodon elipsonoides* and *Phoradiadus divortiensis*. The entoconid is reduced and coalescent with a very short hypoconulid. Labial fold (ectoflexid) and lingual folds (meta and entoflexid) very well developed. The ectoflexid is deeper and more penetrating than the lingual flexids, with the entoflexid more open than the metaflexid. Well-developed anterior and posterior cingula extend labiolingually and may or not be connected to the labial and lingual cingula. The labial cingulum is present in these two specimens, but it is continuous (MLP 04-III-3-1) or is restricted to the base of the labial fold (ectoflexid) (MLP 91-II-4-1). The lingual cingulum is low but continuous (MLP 04-III-3-1) or absent (MLP 91-II-4-1).

A nearly complete right m3, MLP 01-I-1-1 (Fig. 4a), has a trigonid shorter than the more elongated talonid. The trigonid shows the lingual portion of the paralophid engrossed (paraconid or ?neoparaconid) as in the premolars described above, but (at least in this state of wear) with no trace of an independent cusp. The metaconid is the highest cusp and has a relatively wide descending posterior crest. The talonid is more elongated anteroposteriorly than the trigonid, with a posteriorly projected hypoconulid separated by a labial fold forming a short and rudimentary 'third lobe'. The entoconid is bunoid, projects anteriorly and is connected to the hypoconulid; it is more developed and inflated than in *Sparnotheriodon epsilonoides* and similar to ?*V. longidens*, but the entoconid is not so differentiated from the hypolophid as in *Phoradiadus divortiensis*. The ectoflexid is more open, deep and penetrating than the lingual folds, which are relatively shallow. The anterior cingulum is well developed and extends transversely with the lingual portion higher and directed to the paralophid; it is not connected to the labial cingulum that extends from the hypoconulid lobe to the posterior part of the protoconid

column. Some cuspules occur in the ectoflexid valley. The lingual cingulum is apparently restricted to the trigonid, extending from the paralophid to the anterior portion of the metaconid.

Discussion

Notolophus arquinotiensis is one of the most abundant taxa among the terrestrial mammals from the La Meseta Formation. *N. arquinotiensis* is currently represented by a small number of specimens collected at six localities in Seymour Island (Fig. 1). Its tooth anatomy, as described above, is distinctive and allows a clear differentiation from other Palaeocene and Eocene sparnotheriodontids.

Only three sparnotheriodontid genera are so far known in South America (Table 1). A fourth genus, *Heteroglyphis*, from the Mustersan Age (late Eocene) was included tentatively within the family by Soria (2001), although restudy of the type and only known specimen suggests that *Heteroglyphis dewoletzky*, Roth 1899 belongs to the Anisolambdinae or Anisolambdidae eolitopterns. The specimens discussed here were initially referred to *Victorlemoinea* (Bond *et al.* 1990). The genus *Victorlemoinea* was erected by Ameghino (1901), who recognized two species: *V. labyrinthica*, the genotypical one (Fig. 2c) and *V. emarginata*, both based on upper molariform teeth (see Simpson 1948) from the Casamayoran SALMA (possibly Vacan 'subage') of Patagonia. From the same area and age, Simpson (1948) doubtfully referred *Victorlemoinea* to the species *Anisolambda longidens* Ameghino, 1901, based on lower teeth. Later, Paula Couto (1952) referred a fourth species to *Victorlemoinea*: *V. prototypica* from the Itaboraian SALMA (middle Palaeocene) of Brazil and based on upper and lower teeth.

Notolophus arquinotiensis (Fig. 2) is different from *V. labyrinthica*: *V. emarginata* and *V. prototypica* being somewhat larger than *V. labyrinthica*, and definitely larger than *V. emarginata* and *V. prototypica*. The peculiar connection of the protocone–paraloph with the enlarged protostyle is clearly distinct from the morphology observed in the species of *Victorlemoinea*. It is interesting to note that upper molars from the Early Casamayoran SALMA (Vacan subage), referred here as *Victorlemoinea* sp., MLP 66-V-12-2, have a similar size to those of the type of *Victorlemoinea labyrinthica*, but differ in having a smaller hypocone and a shorter crest connecting the metaconule with this cusp. These molars, similar to those figured by Simpson (1948) (i.e. AMNH 28466), also

a

b
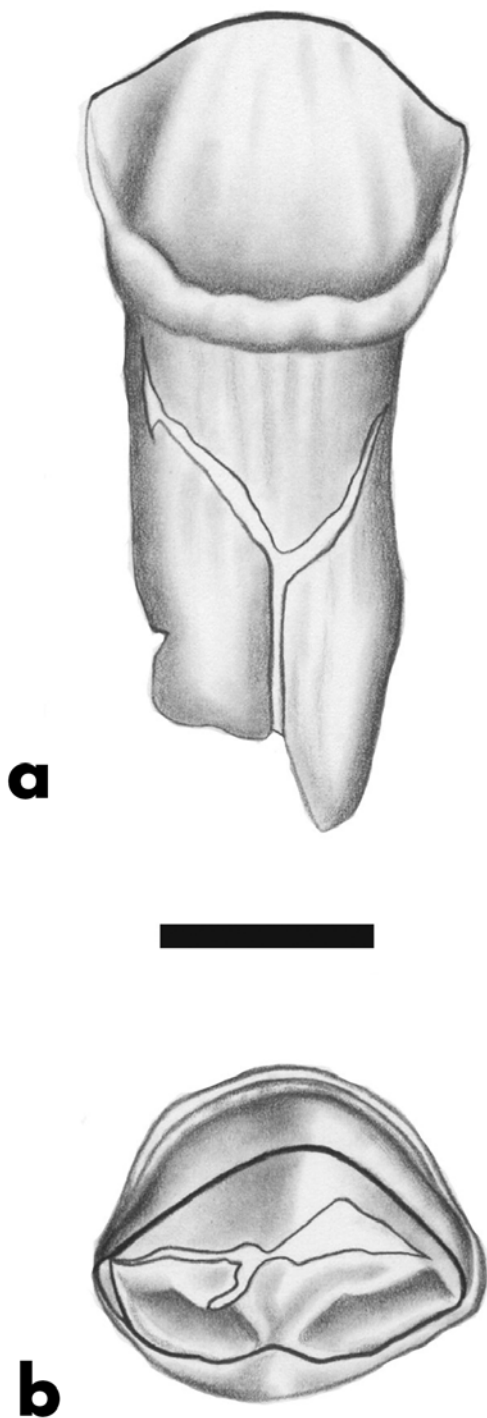
Fig. 5. *Notolophus arquinotiensis*, gen. et sp. nov. MLP 90-I-20-3, right I3?. (**a**) Labial view and (**b**) occlusal view. The scale bar equals 5 mm (drawing by A. Viñas).

from the Vacan subage (Casamayoran age), approach the condition observed in *Notolophus arquinotiensis*, but clearly differ by the paraloph which in MLP 66-V-12-2 is not united to the protostyle as in *V. labyrinthica*.

?*Victorlemoinea longidens* is based on lower premolars and molars not clearly associated. The lower premolars are different from other known Sparnotheriodontidae, and do not have vertically oriented Hunter–Schreger bands; its morphology is more reminiscent of a notoungulate Isotemnidae than a litoptern, and we do not consider this premolar as those of a sparnotheriodontid. The incomplete right lower molars (m1–m2), although of smaller size than those of *Notolophus,* have an enlarged entoconid and a weak lingual cingulum, which are characters also observed in the lower molars of *Notolophus*, but they differ in the more narrow and penetrating meta and entoflexids of ?*V. longidens*. Also, it is very possible that ?*V. longidens* could represent the lower teeth of *Victorlemoinea labyrinthica*.

Sparnotheriodon epsilonoides is only known from its lower teeth and mandible (Soria 1980*a*), so no direct comparison can be made between it and MLP 95-I-10-6. However, the lower molars of the hypodigm of *Notolophus* (MLP 91-II-4-1 and MLP 01-I-1-1) are clearly lophoselenodonts and match very well in size and general anatomy with those of *Sparnotheriodon*.

Recent work on the faunal similarities of the La Meseta fauna indicate a strong biogeographical connection with the southern tip of South America (Patagonia) (Goin *et al.* 1999; Reguero *et al.* 2002), and the identification of archaic marsupial prepidolopids and derorhynchids at Seymour Island reinforces that link. Similarly, the recovery of sudamericid gondwanatheres from Seymour Island and the recognition of strong morphological correspondence between the Seymour gondwanathere and *Sudamerica ameghinoi* also demonstrate a late Palaeocene connection with Patagonia (Reguero *et al.* 2002).

The rare occurrences of sparnotheriodontids in an otherwise very well recorded faunal context of the Palaeocene of Patagonia and Brazil leads to the assumption that they could be extreme ecological specialists. They show a number of dental characteristics that may be adaptations to forested habitats, and the striking dental features of the Antarctic taxon are brachyodonty and the particular structure of the enamel (vertically oriented Hunter–Schreger bands) (Reguero *et al.* 2002). Janis (1984) pointed out that brachyodonty is associated with browsing herbivores that are adapted to forest habitats. In particular, *Notolophus* could

browse, stripping off twigs and saplings from evergreen trees even during winter months (Vizcaíno *et al.* 1998*b*). No post-cranial information is available for the Antarctic ungulates, but information from the nearest relatives (all of them fossils) can be used to infer the locomotor adaptation to the cursoriality. Cifelli (1983*a*, *b*) associated teeth and astragalus and calcaneum to the Itaboraian (Palaeocene) species *Victorlemoinea prototypica* of Brazil.

The faunal evidence, mainly that provided by the marine invertebrates (Stilwell & Zinsmeister 1992), indicates the deposition of the Submeseta Member, where the holotype was recovered, was in cool-temperate conditions, unlike the underlying *Cucullaea* I Member. A sharp decrease of diversity near the contact between the upper members of La Meseta Formation (*Cucullaea* II and Submeseta) may be correlated with the climatic cooling event which culminated at the time of deposition of the uppermost part of the La Meseta Formation (Gazdzicki *et al.* 1992). The presence of *Notolophus*, together with a ground-dwelling bird (ratite) and *Nothofagus* leaves from the same horizon, suggest that the terrestrial environment during the time of deposition of at least part of the Submeseta Member was apparently not dissimilar to that reconstructed by Reguero *et al.* (2002) for the *Cucullaea* I Member with *Nothofagus* forests and mountainous cordillera.

Notolophus had a more bilophodont than bunodont dentition, and their molariforms teeth had strong enamel ridges extending between the cusps. These enamel ridges serve as shearing surfaces, and the formation of dentine 'lakes' along the ridges produce double-edged shearing blades. These mainly performed a shearing action, slicing leaves into quite large pieces like a modern tapir that feeds almost entirely on leaves of forest trees. The body size of the Antarctic sparnotheriodontid (395–400 kg) indicates that it was the largest terrestrial herbivore living in Antarctica at this time (Vizcaíno *et al.* 1998*b*). Evidently, the large size of this herbivore favoured the exploitation of leaves because a longer time in the gut for bacterial fermentation is required to obtain sufficient nutrients from leaves. Based on dental morphology, sparnotheriodontids were probably hindgut fermenters like non-ruminant artiodactyls and perissodactyls (Fortelius 1985; Rensberger & Pfretzschner 1992). Astrapotheres and sparnotheriodontids also have teeth with vertical Hunter–Schreger bands. Fortelius (1985) indicated that a number of lophodont ungulates have evolved vertically oriented Hunter–Schreger bands, a modification that
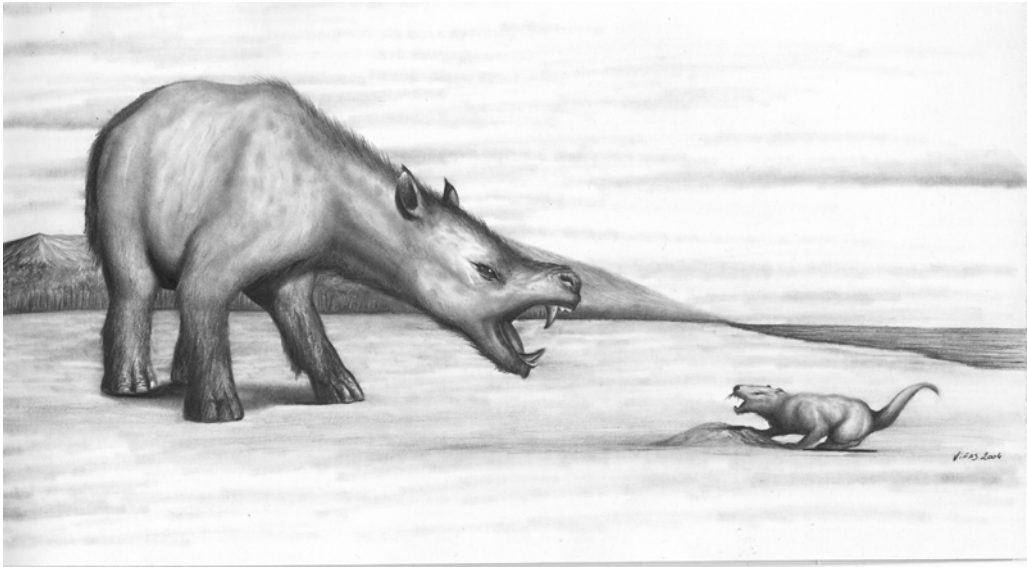
Fig. 6. Reconstruction of the archaic litoptern *Notolophus* and the opossum-like marsupial *Antarctodolops* on the eastern shore of the Antarctic Peninsula during the Middle Eocene. In the background *Nothofagus* forest and mountains (drawing by A. Viñas).

involves the mode of prism decussation and three-dimensional arrangement of the bands. This condition has been interpreted as an adaptation to resist cracking when the enamel edges are loaded in a direction away from the supporting dentine (Boyde & Fortelius 1986). In *Notolophus*, as in the rest of the representatives of the family, the ectoloph forms a thin, vertical, blade-like ectoloph with a strong mesostyle.

Notolophus arquinotiensis is a large sparnotheriodontid (Fig. 6), larger and different in morphology than the last ones of the Divisaderan SALMA (late Eocene), and more similar in size to some remains of the Vacan Subage (Casamayoran Age; early Eocene). The material of *Notolophus* from Seymour Island exhibits no change of size through the Campamento Member (TELM 3) to the Submeseta Member (TELM 7) of the La Meseta Formation, indicating that the individuals of *Notolophus arquinotiensis* were of very large size existing over a large timespan. Also, related forms in the Vacan Subage (early Eocene) may tempt one to propose an immigration event for the sparnotheriodontids in Antarctica near the Vacan Subage or Riochican Age (late Paleocene). However, other taxa (e.g. the marsupials) could indicate an earlier migration datum, but additional taxa from the La Meseta Formation are required to demonstrate either an impoverished fauna of a previous, single immi-

gration event or a cluster of taxa arriving on the Antarctic Peninsula at different times by chance routes.

A more precise reconstruction of the palaeoecology of *Notolophus* would be possible if cranial and post-cranial remains were known. Clearly, much remains to be learned about this rare Antarctic litoptern, questions that only future discoveries of additional material can answer.

Conclusion

The new taxon reported here is the first well-documented Antarctic 'South American ungulate', and it belongs to an archaic and uncommon lineage whose ultimate ancestry may be Laurasiatic 'condylarths'. *Notolophus arquinotiensis* definitively confirms the occurrence of an archaic ungulate population in Antarctica and supports the role of the continent as a probable centre of eutherian evolution (Vizcaíno *et al.* 1998*a*). *Notolophus arquinotiensis* has close affinities with *Victorlemoinea*, indicating at least a very close common ancestor, probably a 'condylarth' despite its strikingly molariform P3–4/p3–4.

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